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Biogeographical patterns in pyrenomycetous fungi and their taxonomy. 2. Additions to the Grayan disjunction

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Abstract — We report additional examples of pyrenomycetous fungi that display the biogeographical pattern known as the Grayan disjunction. *Daldinia grayana* and *Diatrypella informis* are described as new species, and *Nemania pseudoillita* is proposed as a new combination.

Key words — *Ascomycota*, biogeography, new species

Introduction

Additional collecting trips and visits to several different herbaria have revealed a number of specimens that warranted a re-identification. The data available on their distribution indicate that they display the biogeographical pattern known as the Grayan disjunction, which was discussed in a previous paper (Vasilyeva & Stephenson 2010).

Two types of this distribution pattern have been observed in pyrenomycetous fungi—vicariance and non-vicariance. In addition, there are two other groups of fungi restricted to either eastern Asia or eastern North America that do not have close relatives in the other region. Although these two groups of species are seemingly pertinent to the two regions under consideration, the biogeographical patterns they exhibit have different explanations, which will be considered in a forthcoming paper. The purpose of the present paper is to provide additional information relating to the Grayan disjunction in pyrenomycetes and to discuss certain aspects of this pattern.

Materials & methods

The specimens included in this study are deposited in FH, MICH, and VLA. The maps used as the basis for illustrations were taken from the web sites commons.wikimedia.org

(Figs 1–3) and www.paleoportal.org (Fig. 4); all maps were modified to show our data. Photographs of ascomata were obtained using a Nikon D40x digital camera.

Examples of the non-vicariance pattern

Daldinia grayana Lar.N. Vassiljeva & S.L. Stephenson, **sp. nov**. Fig. 1

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Stromata solitaria vel aggregata et confluentia, sessilia vel breve stipitata, 0.5–2.5 cm diam. × 0.8–2.5 cm alta, atro-lateritia, demum denigrata et laccata, rugosa, epapillata et sine tumulis peritheciorum, pigmenti griseo- vel veriduli-olivacei, interdum atro-gresei vel plumbei in KOH dissoluti; textura sub peritheciis zonis alternantibus composita, zonis fuscis 0.3–0.6 mm crassis et zonis cremeo-fuscis 0.1–0.3 mm crassis praedita. Perithecia tubularia, 0.1–0.2 mm diam. × 0.4-0.8 mm alta. Asci partibus sporiferis 80–100 × 7–8 µm, stipitibus 80–100 µm longitudine, annulo apicali in liquore iodato Melzeri cyanescente, discoideo, 3–4 × 0.8–1 µm. Ascosporae brunneae, unicellulares, brevi- et late-ellipsoideae vel anguste-ellipsoideae, apicibus anguste-rotundatis, (10–)12–14(–16) × 6–7.5 µm, rima germinativa recta longa praeditae; perisporium in KOH dehiscens, leve.

Type: Russia: Primorsky Territory, Lazo Nature Reserve, on *Alnus hirsuta* (Spach) Turcz. ex Rupr. (*Betulaceae*), 4 Aug 1986, *L. Vasilyeva* (**Holotype** VLA P-2547).

Stromata solitary to aggregated and confluent, sessile or short stipitate, 0.5–2.5 cm diam., 0.8–2.5 cm high, dark reddish brown, blackened and varnished in age, wrinkled, lacking papillae and perithecial mounds, KOH-extractable pigments gray-olivaceous or greenish-olivaceous, sometimes dark-gray or plumbeous; tissue below the perithecial layer composed of alternating zones, the darker zones dark brown, 0.3–0.6 mm thick, the lighter zones creamy-brown, 0.1–0.3 mm thick. Perithecia tubular, 0.1–0.2 mm diam. × 0.4–0.8 mm high. Asci in the spore-bearing part 80–100 × 7–8 µm, the stipe 80–100 µm long, with apical ring bluing in Melzer's iodine reagent, discoid, 3–4 × 0.8–1 µm. Ascospores brown, unicellular, variable in shape, broadly ellipsoid to more narrow-ellipsoid, (10–)12–14(–16) × 6–7.5 µm, with a straight germ slit spore-length; perispore dehiscent in 10% KOH, smooth.

Additional specimens examined: **CHINA**: **Heilongjiang Province**, Raohe, on *Alnus hirsuta*, 7 Aug 2004, *L. Vasilyeva* (VLA P-2551). **CANADA**: **Nova Scotia**, Salmon River, 14 Jul 1931, *L.E. Wehmeyer* (MICH 71984, as *Daldinia concentrica*). **USA**: **New York**, Ithaca, Aug 1902, *C.H. Kauffman* (MICH 71986, as *Daldinia concentrica*; substrate not indicated); **Vermont**, Pawlett, on *Betula papyrifera* Marshall (*Betulaceae*), *C.W. Dodge & D.H. Linder* (FH, as *Daldinia concentrica*); **Michigan**, Vermilion Point, 30 Jul 1914, *A.H. Povah* (MICH 71987 & 71988, as *Daldinia concentrica*); Rock River, on *Alnus* sp., 24 Aug 1927, *A.H. Povah* (MICH 71989, as *Daldinia concentrica*); SE of Stockbridge, on dead wood, 20 Aug 1928, *E. Whitney & B.B. Kanouse* (MICH 71992, as *Daldinia concentrica*); Rock Harbor, on *Betula papyrifera*, 20 Apr 1930, *A.H. Povah* (MICH 71990, as *Daldinia concentrica*); Todd Harbor, on *Alnus* sp., 24 Aug 1930, *A.H. Povah* (MICH 71985, as *Daldinia concentrica*); McCargoe Cove, on *Alnus* sp., 1930 (date not indicated), *A.H. Povah* (MICH 71982, as *Daldinia concentrica*); Conway Lake Road, on *Betula alleghaniensis* Britton, 12 Aug 1970, *K.A. Harrison* (MICH 71983, as *Daldinia concentrica*); Pine Lake, on *Betula* sp., 23 Jul 1971, *K.A. Harrison* (MICH 71991, as

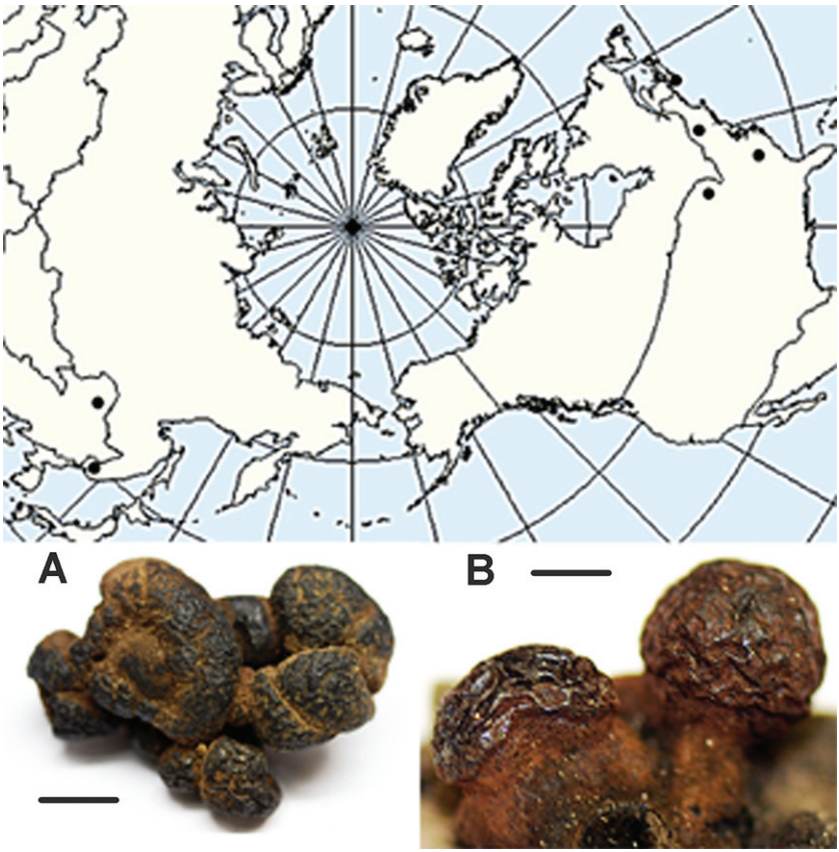

Fig. 1. Approximate biogeographical distribution of *Daldinia grayana*. Scale bars: A = 10 mm, B = 5 mm.

Daldinia concentrica); **Tennessee**, Smoky Mountains National Park, Newfound Gap, on *Betula* sp., 13 Aug 1968, *D.A. Reid* (K, as *Daldinia vernicosa*).

Comments–The appearance of *Daldinia grayana* is similar to that of *D. gelatinosa* Y.M. Ju et al. as the latter is illustrated (Ju et al. 1997, Fig. 44) and described (Ju et al., 1997, p. 270: "Stromata... sessile or short stipitate, solitary or aggregated, wrinkled, ...surface dark brick, blackened and varnished in age..."). It is also noteworthy that *D. gelatinosa* appears to have a similar distribution in eastern North America and is reported from Ontario (Canada), Idaho, and New Hampshire. The latter record is associated with *Betula alleghaniensis*, as is one record of *D. grayana*.

The resemblance of *Daldinia gelatinosa* to *D. grayana* is reinforced by the fact that one piece of the exsiccate of '*Daldinia concentrica*' in Ellis & Everhart's

"Fungi Columbiani 213" was identified as *D. gelatinosa* (Ju et al. 1997: WSP 1781), whereas we identify another piece (MICH 71993) as *Daldinia grayana*. Except for this questionable material, *D. gelatinosa* differs from *D. grayana* in having dark-livid KOH-extractable pigments rather than gray- or greenish-olivaceous pigments, as well as in the nature of the inner tissue of the stromata. This tissue in *D. gelatinosa* is similar to that of *D. fissa* Lloyd in having the alternating zones of dark brown and white, which are initially gelatinous but disintegrate and become loculate when dry. In contrast, *D. grayana* has stromata that are solid inside, and their alternating zones are only darker and lighter tinges of brown, although sometimes the lighter zones are cream-colored.

Based on the abundant material from Michigan, *Daldinia grayana* might be more of a northern or high elevation species (cf. the record from Newfound Gap) than *D. gelatinosa*; in this respect, *D. grayana* is similar to *D. loculata* (Lév.) Sacc., which occurs on birch (*Betula* spp.) in the more northern parts of the Holarctic; when *D. loculata* is found in more southern regions, it occurs primarily in the mountains.

In terms of the substrate preferences (*Alnus* spp., *Betula* spp.), *Daldinia grayana* should be also compared with *D. decipiens* Wollw. & M. Stadler, which is known to occur on *Betula* spp. in Europe (Stadler et al. 2001b), and *D. petriniae* Y.M. Ju et al. described on *Alnus* also from Europe (Ju et al. 1997) but later found to be circumpolar (Stadler et al. 2001b, p. 175). Only one locality for *D. petriniae* in the United States is from the Pacific coast region (Stadler et al. 2001a, c). This species differs from *D. grayana* in having larger, more fragile stromata, livid purple or dark livid pigments, and a finely papillate stromatal surface (similar to the condition illustrated by *D. childiae* J.D. Rogers & Y.M. Ju as seen on the website http://mycology.sinica.edu.tw/Xylariaceae). We have a specimen of *D. petriniae* on *Alnus hirsuta* from China (Heilongjiang Province) collected in 2004. The pigments in its stromata display pale-vinaceous-grey pigment in 10% KOH instead of livid purple or dark livid, but it is the same portion of the color spectrum in contrast to greenish-olivaceous tints observed in *D. grayana*.

Daldinia decipiens is similar to *D. petriniae* in having purple, dark livid or vinaceous purple KOH-extractable pigments (Stadler et al. 2001b). Morphologically, these two species are sometimes difficult to distinguish, although *D. decipiens* appears to have larger ascospores; it also differs from *D. petriniae* in the smaller, often stipitate, stromata with a smooth surface and more solid inner tissue with brown zones of very close tinges. In addition, the stromata of *D. decipiens* are reddish brown, especially the stalks, whereas those in *D. petriniae* are mostly brown vinaceous. The color is shared by *D. decipiens* with *D. grayana*, but the stromatal pigments and consistency easily distinguish them.

Diatrypella informis Ellis & Everh. ex Lar.N. Vassiljeva & S.L. Stephenson, **sp. nov.**

MycoBank MB 561655

Stromata solitaria vel aggregata, e cortice erumpentia, linea nigra substrato circumdata, verrucaeformia, plano-convexa, suborbicularia vel ellipsoideae, 4–10 × 1.5–4 mm, laeviuscula vel leviter rugosa, nigra, intus albida. Perithecia subglobosa, 0.1–0.2 mm diam., profunde immersa, cum ostioli integri, umbilicati vel leviter papillati, Asci longe ellipsoidei vel clavati, polyspori, aparaphysati, partibus sporiferis 35–60 × 5–7 µm, stipitibus ad 75 µm longitudinus, tunica apice incrassata, annulo apicali nullis. Ascosporae allantoideae, unicellulares,brunneolae vel flavidae, 4–6 × 1–1.2 µm.

Type: Ellis & Everhart's North American Fungi N 2530: "*Diatrypella informis* E. & E. n. sp., on dead *Carpinus*, London, Canada, Apr. 1890, J. Dearness". [**Holotype** BPI].

Stromata usually densely scattered over the branches of the host tree, surrounded by a black zone, erumpent from the bark with a black, robust, rounded or ellipsoid, convex, smooth or somewhat wrinkled ectostromatic disc 4–10 × 1.5–4 mm in diam. Perithecia subglobose, 0.1–0.2 mm diam., deeply immersed, the tissue above perithecial layer white, ostioles umbilicate or slightly papillate, non-sulcate. Asci long ellipsoid or slightly clavate, polysporous, in the spore-bearing portion 35–60 × 5–7 µm, stalks up to 75 µm, wall thickened at the apex, without an apical ring and paraphyses. Ascospores unicellular, allantoid, brownish yellow when crowded in asci, pale yellow when scattered, 4–6 × 1–1.2 µm.

Additional specimens examined: **RUSSIA**: **Primorsky Territory**, Vladivostok vicinity, on *Carpinus cordata* Blume (*Corylaceae*), 6 Jun 1958, *I. Bunkina* (VLA P-1975); 11 Oct 1991, *L. Vasilyeva* (VLA P-1978 & P-2129); 5 Oct 2006, *L. Vasilyeva* (VLA P-1108); Sikhote-Alin Nature Reserve, on *Carpinus cordata*, 24 Oct 1985, *L. Vasilyeva* (VLA P-2126); Kedrovaya Pad Biosphere Reserve, on *Carpinus cordata*, 4 Oct 1987 & 25 Oct 1987, *L. Vasilyeva* (VLA P-2127 & P-2128); Ussuriysk Nature Reserve, on *Carpinus cordata*, 19 Aug 1989, *L. Vasilyeva* (VLA P-2265); Anisimovka, on *Carpinus cordata*, 20 Sep 1996, *L. Vasilyeva* (VLA P-2130).

Comments– *Diatrypella informis* was illustrated in the previously published paper on biogeographic patterns in pyrenomycetous fungi (Vasilyeva & Stephenson 2010), but its name was never validly published. Therefore, a Latin description is provided herein to validate the name.

The rather large robust stromata and non-sulcate ostioles of *D. informis* are similar to those found in *D. verruciformis* (Ehrh.) Nitschke, which differs by possessing larger asci (120–200 × 8–12 µm: Nitschke 1867) and longer ascospores (6–8 µm long). The 4–6 µm range in ascospore length is used to segregate many species in the *Diatrypaceae*; examples include *Diatrype hypoxyloides* De Not., *Diatrypella decorata* Nitschke, *Eutypa mela* (Schwein.) Cooke, *Eutypella kochiana* Rehm. The regularly repetitive size ranges in different genera of the family are always very helpful in delimiting certain species within these families.

Examples of the vicariance pattern

Hypoxylon dearnessii and *H. massulatum*

Collections carried out in the vicinity of the University of Michigan Biological Station (UMBS, located near Douglas Lake, Michigan) in 2010 revealed a *Hypoxylon* species with rather variably shaped, often undulate stromata. This species was associated with *Acer rubrum*. Some of its superficial features suggested *Hypoxylon dearnessii* (Ju & Rogers 1996: Figs. 11A–B), recorded from maples only in eastern temperate North America and originally described from the vicinity of the city of London (Ontario, Canada) in the same general Great Lakes region as the UMBS area.

The KOH-extractable pigment in the Michigan specimen was the color of sienna (as in *H. dearnessii*), and the ascospores exhibited a similar size range (9–11.5 × 4.5–6 µm), although with a slightly larger range in length (9–12.5 × 4.5–5.5 µm) and with many more obovoid with one end narrowly rounded and the other broadly rounded, as in *H. fuscopurpureum* (Schwein.) M.A. Curtis. *Hypoxylon fuscopurpureum* differs in having greenish-olivaceous pigments and larger ascospores, but it and the Michigan specimen both have perispores that are indehiscent in 10% KOH. The perispore is important in delimiting *Hypoxylon* species and, in fact, prevents our assigning the Michigan specimen to *H. dearnessii*, which has a dehiscent perispore. Nonetheless, the specimen is provisionally identified as *H. dearnessii* (VLA P–2519) and is accessible for future comparative studies.

Hypoxylon dearnessii is known from Canada (Ontario, Quebec) and the United States (Colorado, Maine, New York) (Ju & Rogers 1996; Stadler et al. 2008). Specimens deposited in the Farlow Herbarium (all as '*Hypoxylon rubiginosum*'), were collected in Connecticut, Massachusetts, New Hampshire, Rhode Island, and Vermont, mostly on *Acer rubrum*. The eastern North American temperate zone is home to *H. dearnessii*, but there are some collections from eastern Asia that resemble this species. Especially suggestive is a specimen collected in 2000 on *Acer ukurunduense* from the Big Khekhtsir Nature Reserve (Khabarovsk Territory, Russia), because its stromata have the same shape as *H. dearnessii*, and the substrate was maple. However, specimens with the same type of stromata were collected later on *Ulmus* spp. in the Primorsky Territory (Russia) and in Heilongjiang Province (China).

A close examination of the stromata of specimens on *Acer ukurunduense* and *Ulmus* spp. showed their KOH-extractable pigment to be bright red instead of sienna, and they were also found to have smaller ascospores (mostly 7.5–8.5 × 3.8–5 µm) with an indehiscent perispore. Further comparisons showed that these stromata are very similar to those in *Hypoxylon massulatum* described from *Alnus hirsuta* (Vasilyeva 1998).

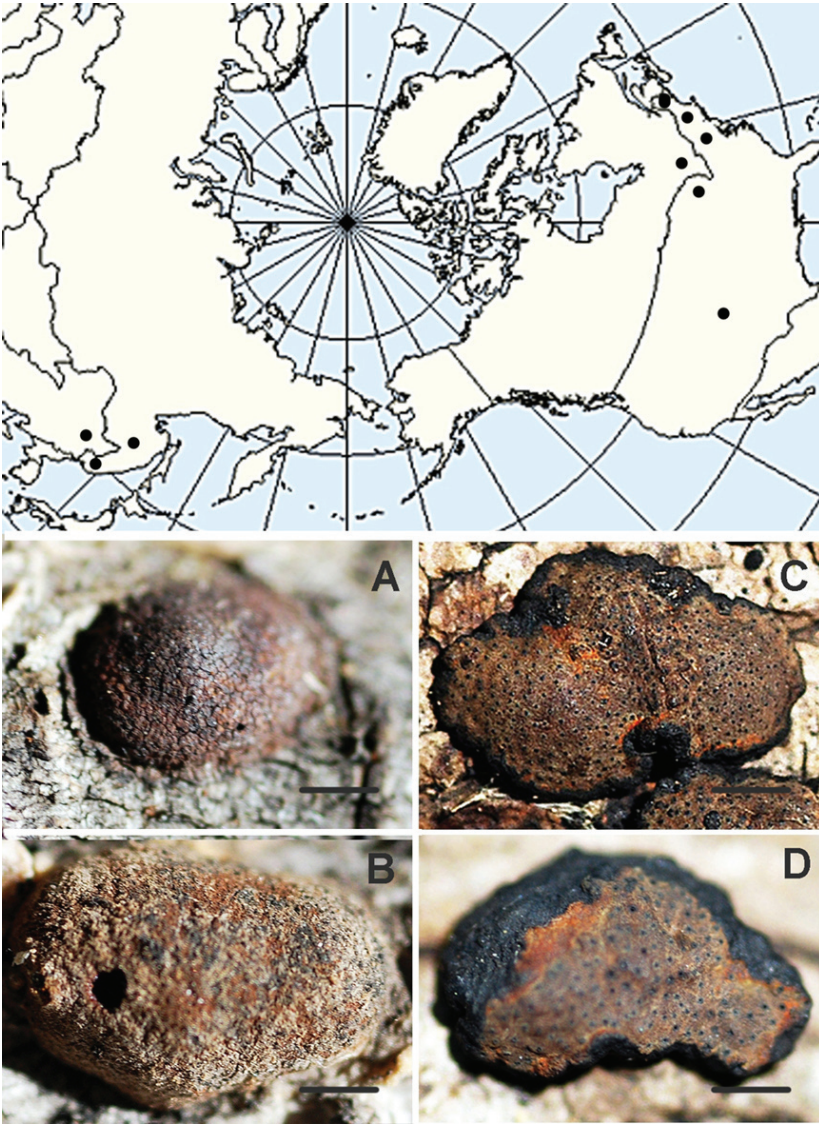

Fig. 2. Approximate biogeographical distribution of *Hypoxylon massulatum* (left) and *H. dearnessii* (right). A–B. *H. massulatum* on *Alnus* (A) and *Ulmus* (B). C–D. *H. dearnessii* on *Acer rubrum* from University of Michigan Biological Station area. Scale bars: A–B = 15 mm, C–D = 10 mm.

Hypoxylon massulatum has been considered as a synonym of *H. howeanum* Peck (Ju et al. 2004), probably because of the similar ascospore size and

stromatal pigments, but its resemblance to *H. dearnessii* (also acknowledged as showing affinities to *H. howeanum*: Stadler et al. 2008) is more evident. *Hypoxylon howeanum* has mostly globose stromata, which are sometimes rather large (up to 2 cm), brightly orange and very smooth at the surface and silky brown inside.

Hypoxylon dearnessii Y.M. Ju & J.D. Rogers, Mycol. Mem. 20: 106 (1996).

Specimens examined: **USA**: **Michigan**, Cheboygan Co., Douglas Lake, University of Michigan Biological Station, on *Acer rubrum* L. (*Aceraceae*), 12 Aug 2010, *L. Vasilyeva* (VLA P-2519); **Connecticut**, New Haven, on *Acer* sp., about 1888, *R. Thaxter* (FH, as *Hypoxylon rubiginosum*); **Massachusetts**, Waverly, on *Acer rubrum*, 23 Apr 1892, *R. Thaxter* (FH); Medford, Middlesex Fells, 13 Oct 1935, *G. Darker* 5479 (FH, as *Hypoxylon rubiginosum*); **Vermont**, Middlebury, Great Swamp, 26 Nov 1896, *E. Burt* (FH, as *Hypoxylon rubiginosum*); **New Hampshire**, near Sawyer's River, on *Acer* sp., Aug 1901, *R. Thaxter* 7112 (FH, as *Hypoxylon rubiginosum*); Chocorua, on *Acer rubrum*, 9 Aug 1907, *W. Farlow* (FH, as *Hypoxylon rubiginosum*); **Rhode Island**, Glochester, substrate not indicated, 6 Jun 1922, *D. Linder & S. Cook* (FH, as *Hypoxylon rubiginosum*).

Hypoxylon massulatum Lar.N. Vassiljeva, Nizshie Rasteniya, Griby i Mokhoobraznye Dalnego Vostoka Rossii, Griby 4: 182 (1998)

Stromata pulvinate, sometimes convex on top, rounded, ellipsoid or irregular, often with crenate margins, 0.4-1 cm diam., surface dark brick, bright orange or ochre; bright red granules immediately beneath surface, with KOH-extractable pigments orange-red. Perithecia ovoid, 200–300 µm diam., ostioles umbilicate. Asci cylindrical, the spore-bearing portion 45–50 × 5–7 µm, the stipes 30-40 µm long, with discoid apical ring bluing in Melzer's iodine reagent. Ascospores one-celled, ellipsoid, pale brown, 7.5–9(–10) × (3.5–)3.8–5 µm, with straight germ slit spore length; perispore indehiscent in 10 % KOH, smooth.

Specimens examined: **RUSSIA**: **Khabarovsk Territory**, Big Khekhtsir Reserve, on *Acer ukurunduense* Trautv. & C.A. Mey., 20 Jun 2000, *L. Vasilyeva* (VLA P-937); **Primorsky Territory**, Nadezhdino District, Sirenevka, on *Alnus hirsuta*, 29 Aug 1991, *L. Vasilyeva* (VLA P-2511); Khanka Nature Reserve, on *Ulmus* sp., 21 Jun 2003, *L. Vasilyeva*, P-936. **CHINA**: **Heilongjiang Province**, Xingkaihu Nature Reserve, on *Ulmus* sp., 1 Sept 2003, L. Vasilyeva (VLA P-1623).

Nemania illita and *N. pseudoillita*

The genus *Nemania* Gray has received attention from a number of mycologists who work with pyrenomycetous fungi (Granmo et al. 1999, Ju & Rogers 2002) but remains rather difficult taxonomically. Seven species in this genus were reported previously from the Russian Far East (Vasilyeva 1998) but as members of the genus *Hypoxylon* Bull.

Hypoxylon pseudoillitum was described as differing from *H. illitum* (Schwein.) M.A. Curtis in having larger ascospores (12-16 against 9-12 µm). The same difference exists between many *Hypoxylon* species (Vasilyeva 1983, 1985). Their stromata also differ (Fig. 3), although it is difficult to differentiate

these species in keys and descriptions. Most probably it is possible to count the number of papilla per unit of surface area, but this feature was usually not taken into account. A new combination for and English description of *H. pseudoillitum* are provided below.

Nemania pseudoillita (Lar.N. Vassiljeva) Lar.N. Vassiljeva & S.L. Stephenson, **comb. nov.** Fig. 3

MycoBank MB 561656

≡ *Hypoxylon pseudoillitum* Lar.N. Vassiljeva, Nizshie Rasteniya, Griby i Mokhoobraznye Dalnego Vostoka Rossii, Griby 4: 190 (1998)

Stromata effuse-pulvinate, plane, with a densely and finely papillate surface, brownish, becoming darker with age; perithecia spherical, 600–800 μm diam.

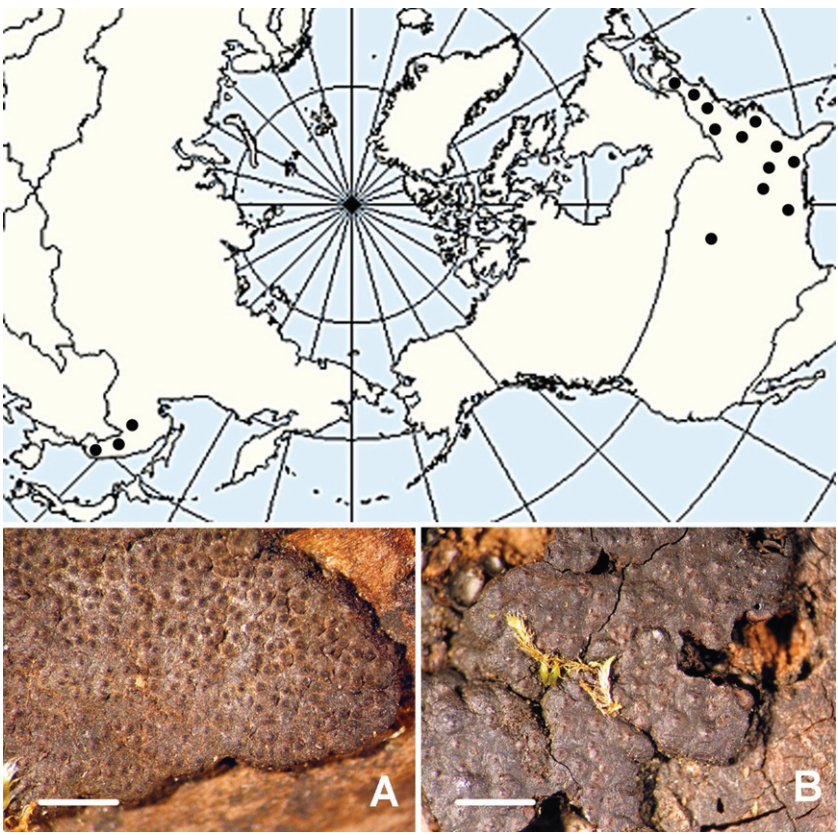

Fig. 3. Approximate biogeographical distribution of *Nemania pseudoillita* (left) and *N. illita* (right). North American localities listed by Miller (1961) include Alabama, Georgia, Kentucky, Louisiana, Maine, Maryland, Missouri, Nebraska, New Hampshire, New York, North Carolina, Pennsylvania, and Virginia in United States. Scale bar = 5 mm.

Asci cylindrical, the spore-bearing portion 80–90 × 5–7 µm, the stipes 40–50 µm long, with apical ring bluing in Melzer's iodine reagent, cubiform, 2 × 2 µm. Ascospores one-celled, diamond- or wedge-shaped, very light brown, almost hyaline, brownish in mass, (11.5–)13–15(–16.5) × (2.5–)3–4.5 µm, with a ventral germ slit.

Specimens examined: **RUSSIA**: **Khabarovsk Territory**, Big Khekhtsir Nature Reserve, on wood, 16 Sept 1981, *L. Vasilyeva* (VLA P-1842); **Primorsky Territory**, Lazo Nature Reserve, on wood, 26 Jul 1986, *L. Vasilyeva* (VLA P-1378); Kedrovaya Pad Reserve, on wood, 28 Oct 1987, *L. Vasilyeva* (VLA P-1380); Ussuriysk Nature Reserve, on wood, 28 Aug. 1989, *L. Vasilyeva* (VLA P-194); Vladivostok vicinity, on wood, 25 May 2003, *L. Vasilyeva* (VLA P-1379).

Discussion

We did not discuss the Grayan disjunction in pyrenomycetous fungi as part of an overview of biogeographical problems in our previous paper (Vasilyeva & Stephenson 2010). Especially interesting in this context is the vicarious pattern. The occurrence of the same species in two widely separate regions of eastern Asia and eastern North America could be attributed to the persistence of Tertiary relics following continental fragmentation, but the occurrence of intercontinental vicarious pairs of species (or varieties) is not so easily understood.

Vicarious taxa usually have very minor morphological differences (e.g., ascospore size), and it is difficult to explain why *Biscogniauxia maritima* Lar.N. Vassiljeva (ascospores 13–16 µm long) occurs only in the southern portion of the Russian Far East, north-east China, Japan, and Korea, whereas *B. atropunctata* (Schwein.) Pouzar (ascospores 24–33 µm long) is restricted to eastern North America. Both species occur on *Quercus* spp., and the ascospore size difference seems unlikely to have adaptive significance. We cannot identify any association between the environmental conditions in the two regions and the observed differences. Moreover, in some vicarious pairs, for example *Nemania illita* and *N. pseudoillita* (see above) or *Hypoxylon notatum* Berk. & M.A. Curtis and *H. ulmophilum* Lar.N. Vassilyeva (Vasilyeva & Stephenson 2010), the species with larger ascospores were found in East Asia. In the latter case, the substrate restriction of *H. notatum* and *H. ulmophilum* to *Quercus* spp. and *Ulmus* spp., respectively, also appears very strange, since representatives of both host genera are abundant in the two disjunctive areas. Although both species have plentiful host resources, they do not seem to jump from one host genus to another in eastern Asia or eastern North America.

Despite their close similarity, vicarious taxa cannot be ancestors and descendants to each other, since, if such is the case, there should be some common area of speciation. And even if such an area existed and became fragmented later, it is inexplicable how such fragmentation has so strictly

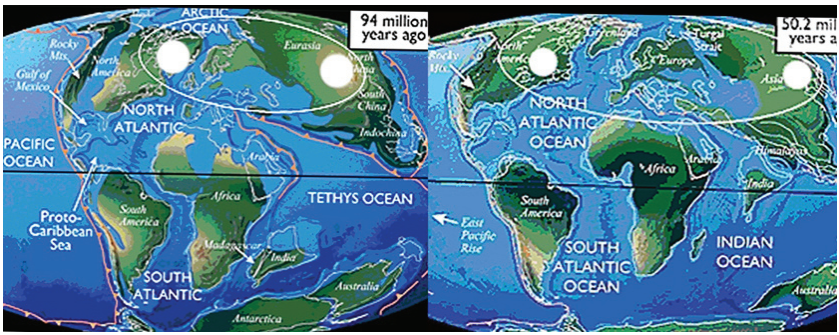

Fig. 4. The position of continents during the Cretaceous (A) and Tertiary (B) periods. White circles indicate the present landmasses of eastern Asia and eastern North America; it is evident that the original isolation of these regions has increased over time.

divided the populations in such a way that all 'ancestors' (with the same ascospore size) appear to be confined to either Asia or North America, whereas all 'descendants' occur on the other region. An additional hypothesis to account for their origin might suggest that only one species existed before continent fragmentation, and the second species evolved as a deviation of the first after long period of isolation of the two regions. However, once again it is not clear why the ancestral species disappeared completely from one fragment of the disjunctive region.

The most probable explanation of the vicariance pattern might be attributed to the position of continents during the Cretaceous and Tertiary periods (Fig. 4). Even during these earlier times, the present land masses of East Asia and eastern North America were widely separated. Therefore, the isolation of vicarious taxa was an original occurrence that only increased over time. The vicarious taxa may have been peripheral populations of some species otherwise widely distributed over Laurasia (the northern part of Pangaea).

It is particularly common for isolated populations at the margins of a range for a given species to exhibit certain distinct features, and clearly distinct peripheral populations are often observed on islands (Ridley 2003). During the Tertiary, the last phase of the breakup of Pangaea, widely separated areas with their own distinctive populations would have became biogeographical 'islands', and the vicarious taxa that exist today may simply represent fragments of the same ancestral species.

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